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The parasitic origin of macroegates among ants

by

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THE PARASITIC ORIGIN OF MACROËRGATES AMONG ANTS.[1]

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THE genus Pheidole among ants is in several respects noteworthy. The unusually large number of species which it comprises afford valuable materials for the taxonomist, while their wide distribution and geographical variation cannot fail to be of interest to the ecologist. Of even greater interest are the certainly very diverse but still imperfectly known habits of the species of this extensive genus. And, finally, a fascinating congeries of morphological and physiological problems centers about the striking dimorphism of the sterile females, or workers of these ants.

In all the known species of Pheidole the worker phase is represented by two very different forms: small-bodied, small-headed, active workers proper, and larger, big-headed, sluggish soldiers. The latter are often of monstrous aspect, and their rôle in the social economy of the various species is still to be worked out in detail.

[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, No. 22.

Until very recently the genus has been characterized as presenting no forms intermediate between the workers and soldiers, in contradistinction to the Old World genus Pheidologeton, the species of which exhibit even in the same colony numerous intermediates between the gigantic, big-headed soldiers and the minute workers. During the past year I found that two of our Texan and Mexican species of Pheidole (*Ph. kingii* André, *var. instabilis* Emery, and *Ph. vaslitii* Pergande) resemble Pheidologeton in presenting, in the very same nest, complete series of intermediates.[1] My attention was directed to this singular condition by Professor Emery, who has described the Texan *Ph. instabilis* from specimens collected at Austin. He has also rectified the synonomy of the Mexican *Ph. tepicana* Pergande, which presents a like polymorphism and has therefore led to the description of several species from soldiers of different dimensions.[2] Recently Professor Forel, utilizing some observations which I made at Queretaro, Mexico, has been able to rectify a similar error in the synonymy of *Ph. vaslitii* Pergande.[3]

In the present paper I desire to call attention to another peculiar modification of the workers of Pheidole, traceable to a perfectly definite, though obviously very different cause from that which must bring about the above-mentioned di- and polymorphism. June 3, 1901, I found at New Braunfels, Texas, on a shady hill that slopes to the lovely sources of the Comal River, two medium-sized nests of *Ph. commutata* Mayr. They were under stones about sixty feet apart. One contained ants of the typical dark variety of the species, while in the other nest both workers and soldiers were decidedly paler. In either case on lifting the stone my attention was attracted by several very large and conspicuous workers with huge abdomens, moving about among the workers and soldiers of normal dimensions. I had been collecting and observing the

[1] Wheeler, W. M. Notices Biologiques sur les Fourmis Mexicaines, *Ann. Soc. Entomol. de Belgique*, tome xlv (1901), pp. 199–205.

[2] Emery, C. Remarques sur un Petit Groupe de Pheidole de la Région Sonorienne, *Bull. Soc. Entomol. de France* (année 1901), No. 5, pp. 119–121.

[3] Forel, A. Fourmis Mexicaines récoltées par M. le prof. W. M. Wheeler, *Ann. Soc. Entomol. de Belgique*, tome xlv (1901), pp. 123–141.

little fungus-growing ants, *Cyphomyrmex rimosus* Spinola, which abounded on the same hill-slope, and all my bottles and bags used for living colonies were filled with these remarkable ants. I was therefore compelled to preserve in some small vials of alcohol as many of the Pheidole workers as could be captured. At the time I supposed that the huge individuals might represent some hitherto unknown guest-ant which had taken up its abode in the nests of the Pheidole.

On returning from my collecting trip I found that the conspicuous individuals were nothing more nor less than gigantic workers of *Ph. commutata*. One of the nests had yielded six, the other three, of these creatures. There were besides from each nest two or three somewhat smaller individuals clearly intermediate in size between the typical and the gigantic workers. All of these large individuals are evidently to be regarded as belonging to Wasmann's category of macroërgates,[1] since they are certainly "individuals which approach the females in an abnormal manner only in the size of the body, but in other respects (even in the development of the abdomen) are normal workers." Although the abdomen is enormously distended in the macroërgates of *Ph. commutata*, it is nevertheless clearly of the worker type.

The length of the normal workers of the Texan *Ph. commutata* is not greater than 3 mm. Many of them are scarcely more than 2.5 to 2.8 mm., which was the length of Mayr's type specimens from Florida.[2] The largest macroërgates, however, measure 5 mm., while the smaller ones are fully 4 to 4.5 mm. long. Thus the volumes of the normal workers and the extreme macroërgates would be in the ratio of 27 to 225 if they had the same form. But the abdomens of the latter are so enormously distended that the ratio must be 27 to at least 200. In other words, the large macroërgates are nearly eight times as large as the normal workers. They are even larger than the soldiers, which measure about 4 mm., though in this

[1] Wasmann, E. Die ergatogynen Formen bei den Ameisen und ihre Erklärung, *Biol. Centralbl.*, Bd. xv (1895), Nr. 16 u. 17, pp. 606–646.

[2] Mayr, G. Die Formiciden der Vereinigten Staaten von Nordamerika, *Verh. d. Zool.-Bot. Ges.*, Bd. xxxvi (Wien, 1886), pp. 419–464.

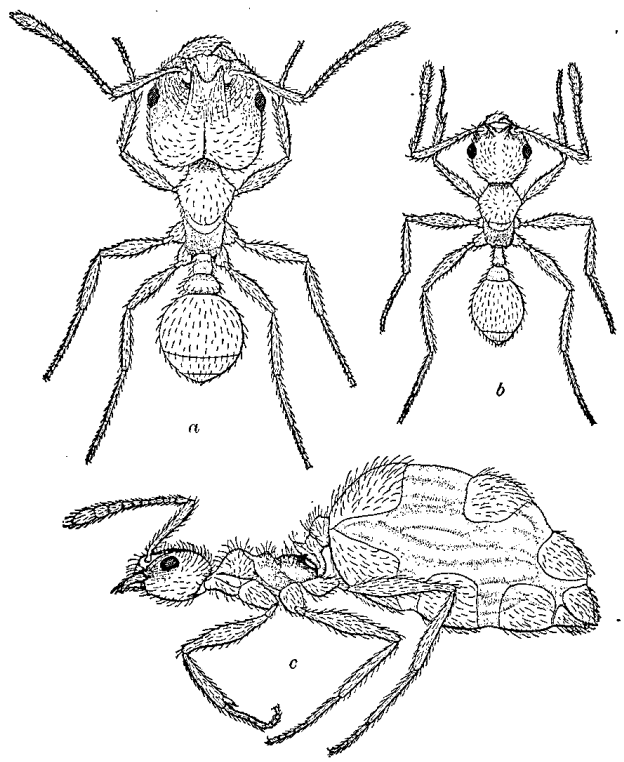
case the difference in size is not so striking on account of the enormous heads of the latter. The size relations are shown in the figures, which represent the soldier, normal and macroërgatic workers, drawn with the camera lucida under the same magnification.

Examination even with a good pocket lens reveals the cause of the great abdominal development of the macroërgates. One sees distinctly the white coils of a parasitic worm distending the abdomen till its dorsal and ventral sclerites are widely separated by the tense intersegmental membranes. Thus the abdomen of the Pheidole comes to resemble externally that of replete individuals of the honey ant (*Myrmecocystus melliger*) or our common northern *Prenolepis imparis*. In some of the alcoholic specimens the tense abdominal wall has burst and allowed a few of the coils of the parasite to protrude. Such specimens may perhaps suggest the way in which the parasite ultimately effects its escape from the ant, if indeed it ever leaves its host.

My friend, Dr. T. H. Montgomery, who has kindly examined a few of the Pheidoles, writes me that the parasite is a species of Mermis. Its exact location in the ant's body is not easy to determine, *i.e.*, whether it occupies the lumen of the enormously distended crop, or ingluvies, or lies in the body cavity outside of the alimentary tract. From careful dissection of a single large macroërgate — the one represented in the figure — I conclude that the Mermis lies *within* the ingluvies. In this case the head of the parasite extended forward through the postpetiolar and into the petiolar segment, thus occupying the attenuated neck of the ingluvies. The fat-body in the parasitized ants is almost or completely absent and the walls of the enormously distended crop are practically in contact with the walls of the abdomen. The large macroërgate figured contained only a single closely convoluted Mermis, which was fully 50 mm. long, or ten times the length of the ant. One individual dissected by Dr. Montgomery contained two somewhat smaller parasites, together with many of their eggs. According to Dr. Montgomery, the parasites are "either fully mature or

in what von Linstow calls the 'second larval stage,' which is, however, really the immature stage." [1]

While it is certainly somewhat singular that a species of Mermis should occur in ants, even greater interest attaches to the case under discussion on account of the manifest effects of the parasite on its host. The fact that all the infested individuals are of huge size as compared with the normal



Pheidole commutata Mayr. *a*, normal soldier; *b*, normal worker; *c*, parasitized macroërgate. (Drawn under the same magnification.)

workers is remarkable, for, on first thought, one would certainly expect an animal infested with such a large parasite to be stunted or, at any rate, below the average stature of the species. This paradoxical condition of the macroërgatic Pheidoles is easily understood, however, when we make due allowance for certain peculiarities in the behavior of ants. In the first place it is obvious that the parasites must enter the body

[1] Von Linstow, O. Das Genus Mermis, *Archiv. f. mikr. Anat.*, Bd. liii (1898).

of the worker ant while she is still a larva. This is proved by the fact that two of the large macroërgates are callows, one of them still very soft and pale yellow, the other — again the one represented in the figure — with harder integument, but without the deep coloration of the mature workers. Such huge parasites could scarcely have made their appearance in ants so recently escaped from their pupæ. But even if there had been no callows among the macroërgates, the truth of the above statement would still be patent, both because the macroërgates were all infested while none of the normal workers were found to contain parasites, and because the stature of an ant is, of course, fixed in the pupal stage and cannot be subsequently increased to the dimensions exhibited in the cases under consideration.

It is evident, furthermore, that the macroërgatic stature, which is very apparent not only in the distention of the abdomen but also in the greater dimensions of the head, thorax, petiole, antennæ, and legs, can have its origin only in an unusually large amount of food consumed during the growth period of larval life.[1] Now, as I have shown in former papers,[2] different species of ants employ very different methods of feeding their larvæ. Species of Camponotus, Formica, Lasius, and Myrmica feed their larvæ with liquid food regurgitated from their crops, and possibly also with the secretion of the salivary glands. Other species, however, like the Ponerinæ and some Myrmicinæ (Aphænogaster, Pogonomyrmex, Tomognathus, and some species of Pheidole), feed their larvæ with comminuted insects. Unfortunately I have not been able to observe the method of feeding in *Ph. commutata*, but it is safe to say that it must conform to one or both of these methods. If the larvæ are fed by regurgitation, we must suppose that the parasitized

[1] The opposite condition, *i.e.*, a small amount of food consumed during larval life, results in what may be called *microërgatic* forms. Such are the firstborn workers of all incipient ant colonies. These forms are, of course, perfectly *normal* products of underfeeding, whereas the macroërgates of Pheïdole are products of overfeeding induced by a *pathological* condition.

[2] Wheeler, W. M. A Study of Some Texan Ponerinæ, *Biol. Bull.*, vol. ii (1900), No. 1, pp. 1–31, Figs. 1–10; and The Habits of Ponera and Stigmatomma, *Biol. Bull.*, vol. ii (1900), No. 2, pp. 43–69, Figs. 1–5.

individuals have some means of informing their nurses that their appetite is unusually keen — like that of a human being infested with a tapeworm. If, on the other hand, the larvæ are fed with comminuted insects, they could simply of their own accord eat much more food than is consumed by the larvæ of normal workers. In either case, however, *the stimulus to the increased feeding that finally results in the macroërgatic stature must, of course, reside in the larva and not in the worker ants which supply the food.*

The ability of a small animal like the worker of *Ph. commutata* to nourish a parasite larger than the normal individuals of the host species is accounted for by the fact that the larvæ and adults of these social insects are so readily fed by other members of the colony. The infested ant therefore suffers relatively little inconvenience when compared with an animal which must rely entirely on its own efforts in securing food. Both during the larval and adult stages the macroërgate must be fed by the other ants, for it is extremely doubtful whether these heavy-bodied individuals ever leave the nest for the purpose of foraging. They probably remain at home like the heavy-headed soldiers.

It is not difficult to understand how the Pheidole larvæ become infested with the Mermis, since the parasite extrudes its eggs within the crop of the adult worker. Such eggs or the embryos arising from them could easily find their way into the gullet and mouth of the ant and be transferred thence to the larvæ while the latter are being licked and cleansed; or, in case the workers of *Ph. commutata* feed their larvæ by regurgitation, the transferring of the parasite would be still easier and more direct.

Other interesting conclusions follow from a consideration of the fact that all the macroërgates are structurally of the pure worker type. Except in the excessive size and peculiar hypertrophy of the abdomen, I can detect no morphological differences between the parasitized individuals and their diminutive sister ants. There is certainly no appreciable tendency to approach the soldier or female type of structure. From this we may conclude either that the larvæ must become infested with

the Mermis after they have developed as workers so far that their structure can no longer be affected except in volume, or that the still undifferentiated larvæ are infested but nevertheless develop into workers because so much of the food which they devour is appropriated by their parasites. A decision between these alternatives would require more precise study than was possible under the circumstances.

While there can be no doubt that macroërgatism in *Ph. commutata* is due to the presence of the Mermis, we cannot with certainty exclude the possibility of an atavistic tendency towards macroërgatism in the workers of this genus; for, as Emery has shown in a very suggestive paper,[1] in those ants which have the sterile females represented by huge soldiers and diminutive workers, the latter have without doubt undergone a reduction in size during phylogenetic development. It would be possible, therefore, to explain macroërgatism as an attempt to regain the ancestral worker stature which was, of course, that of the queen. This is probably the explanation of macroërgatism in many ants, *e.g.*, in Solenopsis, and possibly also in the small group of Pheidole mentioned in the introduction to this paper. While a similar reversional tendency may also be present in *Ph. commutata*, it is perhaps unnecessary to lay much stress upon it, since the presence of the Mermis is of itself quite sufficient to account for the stature of the macroërgates.

It is interesting in conclusion to compare the production of macroërgates in the nests of *Ph. commutata* with certain phenomena observed by Wasmann [2] in mixed nests of *Polyergus rufescens* and *Formica fusca*. He finds that such nests are peculiarly liable to contain ergatoid females of the former species, *i.e.*, "individuals which in size and in the development of the abdomen (even of the ovaries) belong to the true female type, but have the thoracic structure of the workers and are therefore wingless." From a biological point of view these are, as Wasmann claims, really secondary queens. He believes that they are produced by the slave ants (*F. fusca*) through

[1] Die Entstehung und Ausbildung des Arbeiterstandes bei den Ameisen, *Biol. Centralbl.*, Bd. xiv (1894), pp. 53–59. [2] *Loc. cit.*

excessive care and feeding of certain larvæ which had previously been permitted to develop as workers beyond the stage in which the wing rudiments would make their appearance in queen larvæ. In other words, the *fusca* workers attempt to change worker larvæ of Polyergus into queens but succeed only in producing the wingless ergatoids. In explanation of such conduct, Wasmann suggests that the *F. fusca* usually have several queens even in very small nests and may perhaps retain the instinct, when enslaved by Polyergus, to educate numerous female ants. If, after the nuptial flight of the Polyergus, they find no fertile queens of their own species in the nest they may endeavor to transform the young worker larvæ into queens with the above-mentioned result. Wasmann's hypothesis is of interest, as it points to the existence of a peculiar instinct in ants which regulates the number and character of the personnel in the colony. We know that such an instinct is well developed in termites, and it is more than probable that it exists also among ants. It offers an interesting field for future investigation.

Both Wasmann's hypothesis to account for the ergatoid females of Polyergus by excessive feeding of the worker larvæ, and his interesting "Lomechusa-Hemmungs-Hypothese," in which he accounts for the pseudogynes of Formica through an attempt on the part of the ants to transform queen larvæ into workers, seem to start from the assumption that the larvæ are quite passive and that the worker ants feed them entirely in obedience to certain instinctive promptings of their own. This accords with Emery's view [1] that the sexual polymorphism of the ant colony is the result of the development of an instinct in the workers to feed the larvæ in different ways. Hence, "the characters in which the worker differs from the corresponding sexual form are not congenital, or blastogenous, but acquired, *i.e.*, somatogenous. Nor are these characters transmitted by heredity, except as a peculiarity of the germplasma to enter on different paths of ontogenetic development according to the different circumstances of existence." While this view is undoubtedly supported by many facts, and while

considerable importance may indeed be attributed to the initiative of the workers in determining the character of the adult ants which they rear, the macroërgates of *Ph. commutata* prove, nevertheless, that we must also attribute a certain amount of initiative to the larvæ themselves. If this be granted, it is but a short step to the admission that the initiative of the larva, even under normal circumstances, — *i.e.*, when not infested with internal parasites, — may be considerable. It is not altogether improbable that further investigation with this possibility in mind may lead to some alteration or emendation of the various hypotheses that have been framed for the purpose of explaining the complicated phenomena of sexual polymorphism. Thus we may find eventually that the tendency to develop abortive ovaries is really inherited (through the fertile queens of course), and that differences in the chemical nature of the internal secretions, perhaps analogous to those which are supposed to obtain between castrated and non-castrated animals, may furnish the different stimuli that induce the larvæ to demand of their own accord more or less food, or food of a different quality, and to develop accordingly into queens or workers.

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